LOCOMOTOR ORGANS OF ECHINARACHNIUS PARMA

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The method of locomotion in the sand-dollar, *Echinarachnius parma* (Lam.), is not clearly understood. MacBride in the Cambridge Natural History (1906, p. 548) states that "The locomotor tube-feet (in *Echinarachnius*) are very small and feeble compared with those of *Echinus esculentus*, but this is comprehensible when it is recollected how little resistance the yielding sand would offer to the pull of a powerful tube-foot like that of the Regular Urchins, for in order to move the creature through the sand a multitude of feeble pulls distributed all over its surface is necessary, and the locomotor tube-feet are exactly fitted, both as to size and number, for this object." It is quite plain from this quotation that MacBride is of opinion that locomotion in the sand-dollar is accomplished by the tube-feet. In conversation with a well-known specialist in this group of animals, the senior author was informed that *Echinarachnius* possesses no tube-feet at all excepting those that are modified for gills. When experts on the echinoderms differ so widely on a simple question of fact the obvious step is to reinvestigate the subject. The present studies were carried out at the Marine Biological Laboratory, Woods Hole, where an abundance of living specimens of *Echinarachnius* was available.

The locomotion of the sand-dollar has already been reported upon in an earlier paper by the senior author (Parker, 1927). In this publication, it was shown that *Echinarachnius* exhibits two types of locomotion, rotational and rectilinear. In the second type the sand-dollar creeps forward on an axis corresponding to that of its structure. This axis is represented by a straight line passing through the animal and intercepting mouth and anus. Although the animal is in general radially symmetrical, this axis divides it into right and left halves that are structurally significant in its locomotion. In addition to its rectilinear and rotational movements, the sand-dollar can right itself after having been thrown on its back. Such righting reactions also call for an appropriate locomotor mechanism. The question to be discussed in these pages is what structures are concerned with these several types of locomotion. Three classes of organs may be suspected of having to do with such activities. They are the integumentary cilia, the tube-feet (if present), and the spines.

1. *Integumentary Cilia.*—Integumentary cilia have been identified with certainty only on the spines. In *Echinarachnius* the spines are of two kinds, long and short. These two kinds occur on both the oral and the aboral surfaces. The short spines are provided with rounded tops and their cilia occur not only on the tops but also to some extent on their sides. In the long spines the cilia are present as elongated bands on the sides of the spines from the base to near the top. The ends of the long spines are devoid of cilia. It is questionable if any cilia occur on the general surface of the integument, though it is possible that they may be found in the ambulacral grooves. Gislén (1924, p. 247) was unable to demonstrate to his satisfaction the presence of cilia in the ambulacral grooves of the allied *Arachnoides* and *Astriclypeus.*

The direction in which these cilia beat can be determined by the flow of carmine particles discharged on the surface of the sand-dollar. On the aboral face, the ciliary currents flow from the center of the test outward toward the periphery on essentially radial lines anteriorly and posteriorly, but on somewhat curved lines right and left from the axis of locomotion. In these lateral regions the direction of flow is outward and backward. On the oral surface the ciliary currents are all from anterior to posterior, no part of the surface exhibiting currents which run toward the anterior edge. In all cases both oral and aboral, these currents are so weak that they are incapable of moving even small sand particles that happen to fall among them. There is therefore no reason to suppose that the ciliary currents are concerned with locomotion. They function in all probability in the respiratory exchange of water next the animal's body and probably remove from the skin accumulations of very light silt and other dirt.

2. *Ambulacral Feet.*—In a living *Echinarachnius* a continuous fringe of active ambulacral feet can be seen around the whole edge of the test where they are to be observed in incessant activity between the numerous spines. When fully extended, they are two to three times the length of the longer spines. In contraction they draw back close to the general surface of the animal. Each foot is provided with a well-developed terminal sucker deep pink in color. Ambulacral feet essentially like those along the edge may be identified on both the oral and aboral surfaces. Here in consequence of their deep color and characteristic arrangement they give rise to a pattern which in the living animal is often of striking appearance and symmetry. On the oral surface (Fig. 1) they extend as five somewhat irregular bands along the lines of the ambulacral grooves. As these bands approach the edge of the test they widen out till on the very edge they unite to form the continuous fringe already mentioned. On the aboral surface

(Fig. 2) five well-defined double ambulacral bands of tube-feet extend from near the center of the test to its edge. Each double band passes between the two halves of a respiratory rosette. A few tube-feet are often to be seen among the gills on the outer edges of the rosettes. As the double bands approach the periphery of the test they are supplemented on each side by double series of three or more large spots, containing many tube-feet. The double bands and the supplemental spots as they approach the margin expand to such a degree that they form the continuous edging of tube-feet already described. In general the tube-feet are especially numerous and long on the edge of the test, and fewer and shorter toward the center. The shortest and least active feet occur in the ambulacral grooves. Except in the

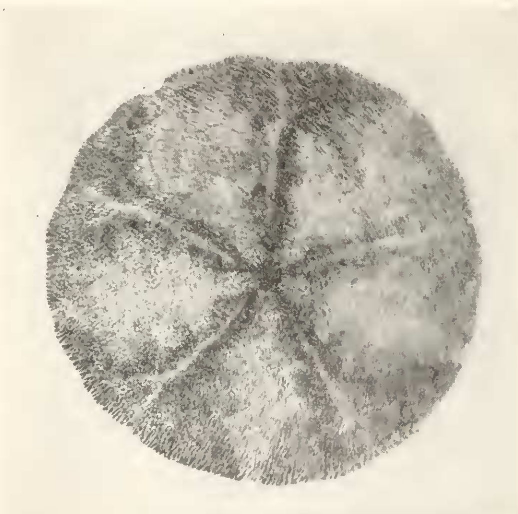

FIG. 1. Oral view of a living *Echinarachnius parma*. The dark areas beginning at the mouth and following the ambulacral grooves to the edge of the test near which they expand broadly and somewhat irregularly are the areas covered with ambulacral feet.

regions previously noted we have found no ambulacral feet in *Echinarachnius.*

When a sand-dollar moves forward on the sand in process of burrowing, the tube-feet of the anterior edge pull the grains of sand in toward the center of the animal, particularly over the anterior half of the periphery. The action of the feet is not vigorous nor well coördinated. Those along the advancing edge are most active and succeed in piling the sand into a low mound on the front of the animal. In moving forward, the animal pushes itself under this mound and the tube-feet help thus to cover the aboral surface. It was difficult to determine the direction of pull of the feet in the middle of the oral side. When a sand-dollar was placed in a glass vessel and studied from below by means of a low-power microscope, the feet were seen to move less regularly than those along the edge of the test. In order to observe the movements of such feet, it was necessary to reduce the sand on the bottom of the glass to a very thin layer. This was unfavorable for the movements of the animal and may have been the occasion of the irregular movements seen under these circumstances. Possibly in deep sand the more centrally located feet would have shown a very different

FIG. 2. Aboral view of a living *Echinarachnius parma*. The five pairs of radial dark bands and the marginal and submarginal dark spots are the areas covered with ambulacral feet.

type of movement. The pulls of the feet on the posterior portion of the test were toward the mouth, but they were feeble and less coördinated than those of the anterior edge.

There is thus no doubt of the presence of tube-feet on *Echinarachnius*, but it is improbable that the forward locomotion of this animal is in any essential way dependent upon them. In this respect our results fail to support the opinion already quoted from MacBride. The only part of *Echinarachnius* in which the tube-feet exhibit well coördinated and vigorous activity is along the anterior edge of the test, but even here their number and distribution is such that they cannot be regarded as more than subsidiary organs in the locomotion of this animal.

3. *Spines.*—The test of *Echinarachnius* is covered thickly with two kinds of spines, long and short. The only parts of the surface that lack spines are the troughs of the ambulacral grooves on the oral surface. The spines are longest near the anterior oral edge and diminish somewhat in size as one passes posteriorly from this region. As one approaches the posterior edge larger spines are again met with, but these posterior spines never reach in size those of the anterior margin. On the aboral surface the spines for the most part point toward the margin of the test, hence radially. On the oral surface the arrangement is less simple, but on both surfaces the spines exhibit a bilateral distribution in relation to the axis of locomotion. This arrangement of the spines has already been figured (Parker, 1927, Fig. 1). When a sand-dollar is placed on submerged sand, it will push forward into the sand until in 10 to 20 minutes it has covered itself completely. This operation involves forward locomotion through about ten centimeters of distance. After the sand-dollar has become covered it usually progresses less rapidly and may in fact stop moving altogether. As the animal moves forward in burying itself, the sand, as already stated, piles up over the anterior edge and gradually spreads over the aboral surface to the complete disappearance of the animal. This is due particularly to the forward movement of the animal as a whole and partly to the pull of the ambulacral feet. When sand is poured on the central part of the aboral surface of an animal submerged in water, it is spread over that surface in radial directions and this spread is dependent upon the movement of the spines of the surface.

When an animal in process of burying itself is observed through very shallow sand from the under side, the spines are seen to exhibit a striking activity. Waves of spine movement begin along the anterior border and sweep backward over the aboral surface of the animal toward the mouth and along the lateral edges of the test to the posterior region. These waves pass in one direction only. They are the result of coördinated movements of the spines, each one of which carries out a relatively complex stroke. Apparently the individual spine swings on its facet from anterior to posterior in a vigorous vertical stroke. It returns to its initial position not by a simple reversal of this movement but by a sidewise swing in a plane near that of the general surface of the test until it has reached its starting point, when a second vertical stroke takes place followed by a lateral recovery. This can be demonstrated in part by placing an inverted sand-dollar in water shallow enough barely to cover its recumbent spines. Under such circumstances waves of spine movements can be seen passing over the anterior oral surface, and the tips of the spines as they cut the water in these waves appear always to be moving posteriorly. No spine tips in the return stroke are seen, for this is accomplished entirely under the water. These coördinated movements of the spines on the oral surface are the occasion of the animal's locomotion. Forward progress, burrowing, and righting movements of the sand-dollar are to be explained by the vigorous and well coördinated movements of these particular spines. The longest and most active spines of the anterior part of the oral side are the chief means to this end. The ambulacral feet are at best only a weak supplement to these movements.

Summary

1. The integumentary cilia in *Echinarachnius* cover the tips of the short spines and the sides of the long ones. On the oral surface they beat radially; on the aboral they beat from anterior to posterior. They play no essential part in the locomotion of the animal, but are probably concerned with feeding, with cleaning the outer surface, and with the respiratory currents.

2. The ambulacral feet form five complicated radial bands on the oral and the aboral sides of the test and a complete marginal fringe. Their tips are deep pink and provided with suckers. They are significant in locomotion to only a limited extent in that on the anterior edge of the test they pile up the sand on the aboral surface.

3. Spines cover the oral and aboral surfaces. They are of two types, long and short. They are best developed over the anterior portion of the oral surface where their distribution exhibits bilateral symmetry in relation to the axis of locomotion. In this region waves of coördinated spine movement pass from the anterior edge of the test posteriorly. In these waves each spine makes a vigorous posterior thrust in a vertical plane and an unimpeded recovery in a plane more nearly lateral. Forward locomotion, burrowing, and righting are types of motion dependent primarily on these spine movements.

References

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